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Whip spiders (Arachnida, Amblypigi) from Colombian Caves: A review, new records and description of a new species

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Abstract

Subterranean amblypygids, or whip spiders, are important yet understudied components of cave ecosystems, playing key roles as apex predators in these fragile, nutrient-limited environments. Their restricted distributions make them particularly valuable for understanding cave ecosystem dynamics and conservation needs. However, the diversity and distribution of these arachnids in Colombian caves remain poorly documented. This study examines 53 specimens of amblypygids from 12 Colombian caves, and compiles all available literature records to provide an updated list of cave-associated species in Colombia. A new species of *Charinus* is described, based on females collected in a cave in Santander. The genus *Heterophrynus* is recorded from six Colombian caves; *H. yarigui* is newly recorded from Tolima, and for the first time to hypogean microhabitats from Cueva de Los Guácharos, Cunday, Tolima); *H. cervinus* is recorded from Boyacá, Las Cacas Cave, while *H. batesii* is newly recorded from Guaviare Caves in Serranía La Macarena/La Lindosa, Caquetá, and for the first time in hypogean microhabitats. The male gonopodes of *H. guacharo* are described from topotipic specimens from Natural National Park Los Guácharos in the Suaza River basin. *Phrynus araya* is recorded for two additional caves in Santander, and finally *Paraphrynus laevifrons*, is recorded for the first time from Providencia Island and for insular hypogean environments in Colombia from the cave (Cueva Bat Hole, Chay Hill, and Represa Freshwater Bay). These findings expand the distribution of amblypygids in Colombian caves, improve our understanding of their diversity, and provide important data for developing conservation strategies for subterranean ecosystems.

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Keywords
Biospeleology, checklist, hypogean fauna, Pedipalpi

Introduction

Amblypygids, commonly known as whip spiders, are nocturnal arachnids that occupy various microhabitats, including crevices, beneath rocks, fallen logs, termite and ant nest, and even trunks of large trees where they forage at night (Armas and Selter 2013; Giupponi and Kury 2013). They inhabit a wide range of environments, such as tropical rainforests, dry forests, morichales (palm swamps dominated by *Mauritia flexuosa*, typically found in flooded or humid areas), plantations, and anthropogenic areas (Quintero 1981; Armas and Maes 2000; Bloch and Weiss 2002; Armas et al. 2012; Chiriví and Armas 2012; Armas and Selter 2013; Giupponi and Miranda 2016; Vasconcelos et al. 2016; Cubas-Rodríguez and Armas 2023). Notably, amblypygids are frequently associated with caves (Armas and Selter 2013; Torres-Contreras et al. 2019; Moreno-González et al. 2023). Cave-associated amblypygids, found in diverse biomes where caves exist, from tropical rainforest to arid regions, remain understudied, particularly in the context of their ecological and evolutionary adaptations. While many amblypygid species, especially those in the genus *Charinus*, are often short-range endemics, some species, such as those within the genera *Heterophrynus*, *Phrynus*, and *Paraphrynus*, can occupy broader geographic ranges.

The ongoing global decline in biodiversity (Cowie et al. 2022), along with shifts in species distributions driven by climate change and other human interventions (Chen et al. 2011; Lenoir et al. 2020), highlights the critical need to document contemporary species distributions as a baseline for future research and conservation. This is particularly relevant for amblypygids, as their ecological roles as top predators (Chapin 2019) and their sensitivity to environmental changes make them important indicators of ecosystem health. By studying these arachnids, especially in understudied habitats like caves, we can better understand their adaptations, distributions, and conservation needs in the context of ongoing environmental and climatic changes.

Caves are important ecosystems that harbor unique and often endemic species. Importantly, subterranean ecosystems are increasingly impacted by diverse human activities, including climate change (Vaccarelli et al. 2023), threatening this unique biodiversity (Mammola et al. 2019). Amblypygids are commonly reported in faunistic surveys of caves, playing important ecological roles as apical predators (Araújo et al. 2019; Chapin 2019). Some species exhibit troglomorphic traits, such as elongated appendages and depigmentation, reflecting strict adaptation to hypogean conditions (e.g. Delle-Cave et al. 2009; Souza et al. 2024). However, most information on cave-dwelling amblypygids comes from general inventories rather than in-depth studies on their ecology, behavior, or evolutionary significance.

In recent decades, research on amblypygids has advanced significantly, including in understudied countries such as Colombia. Taxonomic studies have led to the discovery and description of new genus and species in Colombia (e.g. Giupponi and Kury 2013; Chirivi-Joya et al. 2020; Seiter and Gredler 2020; Miranda et al. 2021; Moreno-González et al. 2023). Recent efforts have also proposed a homologous system and standardized nomenclature for male genital structures, providing critical tools for resolving taxonomic complexities within the group (Giupponi and Kury 2013; Löscher et al. 2022). Beyond taxonomy, amblypygids have been locally studied from various diverse perspectives, including intraspecific morphological variation in Colombian populations (Vásquez-Palacios and Chirivi-Joya 2023), ecological analyses of distribution and abundance patterns (e.g., Bloch and Weiss 2002), and predictive habitat modeling in Colombia (Vásquez-Palacios and Chirivi-Joya 2023).

Prior to this study, approximately 19 species of amblypygids were documented in Colombia, with seven reported from hypogean environments. Among these, the genera *Heterophrynus* Pocock, 1894a and *Phrynus* (family Phrynidae) are notable for their relatively wide distributions in subterranean ecosystems (e.g. Chapin 2019). Other cave-associated genera, as such *Charinus* and *Jorottui*, exhibit more restricted distributions, often limited to single localities. Despite this growing information, we still lack a comprehensive synthesis consolidating existing knowledge and providing updated records of amblypygids in Colombian caves. This synthesis is crucial, as amblypygids are top predators in caves, contributing to maintain ecological balance. Additionally, species with restricted distributions, such as *Charinus* and *Jorottui*, could be particularly sensitive to environmental changes due their narrow ecological niches and limited distribution, potentially serving as sentinels for conservation.

This study addresses this gap by synthesizing all available literature on amblypygids associated with caves in Colombia and presenting new records that extend the known distribution of these species. We examined 53 specimens from 17 collection events—each representing a group of individuals collected together at the same locality, date, and habitat—in 12 caves in karstic and pseudokarstic systems across 8 departments. Key findings include the description of a new species of *Charinus* Simon, 1892 from the department of Santander, description of males gonopods of *Heterophrynus guacharo* Armas, 2015, the first Colombian record of *Paraphrynus laevifrons* (Pocock, 1894b) in hypogean environments, and new records of *Heterophrynus* spp. in Colombia. These results contribute to the understanding of amblypygid diversity in Colombian cave systems and provide a foundation for future research on their ecology, evolution, and conservation.

Materials and methods

We produced a list of Amblypygi species from caves in Colombia based on a comprehensive review of the literature and examination and collection of specimens. All examined specimens are deposited in the collection of the Alexander von Humboldt Institute (**IAvH**), Bogota, Colombia.

Plates of figures were made using Adobe Photoshop CS program, based on digital photographs taken with a Leica M205C stereoscope attached to a Leica DFC450 digital camera. The map was made using the software ArcGIS® 10.1 (ESRI 2024). Description of *Charinus* sp. nov. follows Miranda et al. (2021). The pedipalp morphology follows Harvey and West (1998) as explained in Miranda et al. (2021), and genital nomenclature follows Giupponi and Kury (2013) and Seiter and Gredler (2020). The abbreviations used in the text and figures are: **LaM** = lamina medialis; **Fi** = fistula; **LoD** = lobus dorsalis; **LoL1** = lobus lateralis primus; **LoL2** = lobus lateralis secundus; **PI** = processus internus.

Terminology for specimen records follow the Darwin Core (DWC) standard, allowing for interoperability with the Global Biodiversity Information Facility and other biodiversity resources. For literature-derived data, only locality, coordinates, elevation, and original reference(s) are provided to avoid redundancy, as full details remain accessible in the primary sources.

Results

Taxonomy

Family Charontidae Simon, 1892

Charinus rocamadre Torres-Contreras, Álvarez & Armas, 2015

Records. Colombia: Sucre, Cueva Roca Madre (Torres-Contreras et al. 2015; Torres-Contreras et al. 2019).

Charinus santandereanus sp. nov.

https://zoobank.org/65C275B6-98C6-49ED-A3D8-E6DF263EFA21
Figs 1A–K, 2A, B, 14A, 15

Diagnosis. Due to the exceptional species diversity and high endemism in *Charinus*, the diagnosis compares the new species with all three Colombian congeners (*C. miskito*, *C. rocamadre*, and *C. mocoa*) for regional differentiation, as well as with geographically proximate Venezuelan species that share its median-eyeless condition, ensuring comprehensive morphological and biogeographical context. *Charinus santandereanus* sp. nov. is diagnosed from Colombian congeners by the complete absence of median eyes (vs. reduced eyes in *C. miskito*), two pseudo-articles on leg IV basitibia (vs. three in *C. rocamadre*), and the first cheliceral tooth dentition subequal and dorsal margin concave (vs. dentition heterogenous, ventral denticle enlarged, and dorsal margin straight in *C. rocamadre* and *C. mocoa*). Among non-Colombian Venezuelan median-eyeless congeners, it differs from its morphologically closest relative *C. camachoi* (González-

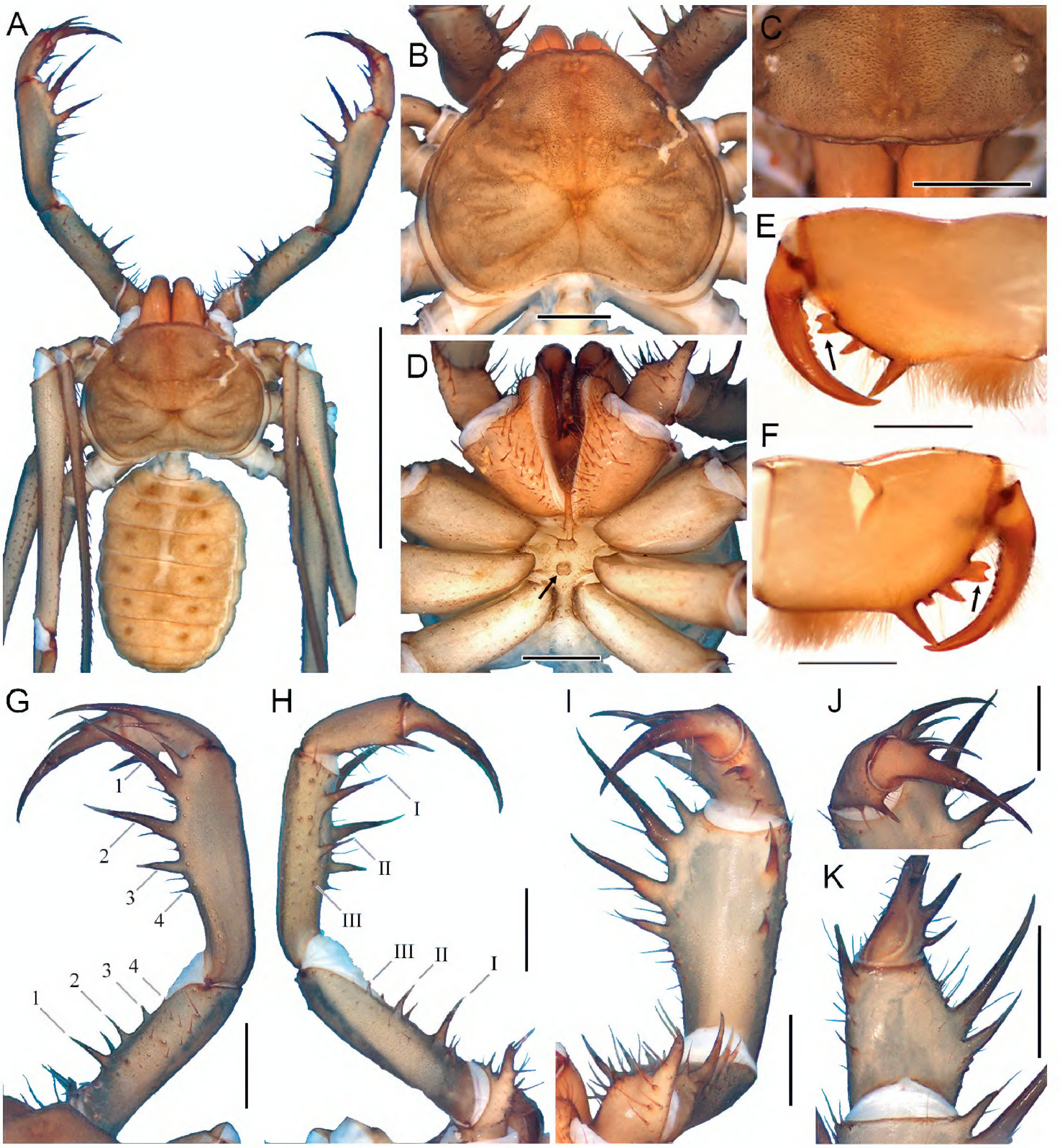

Figure 1. *Charinus santandereanus* sp. nov. (female IAvH) **A** habitus, dorsal view **B** carapace, dorsal view **C** anterior part of carapace, frontal view **D** sternum, ventral view **E, F** right chelicera, mesal (**E**) and ectal (**F**) views **G–K** right pedipalp: dorsal (**G**), ventral (**H**) views **I** left pedipalp, ventromesal view **J** tarsus, dorsal view **K** tibia and tarsus, mesal view. Scale bars: 5 mm (**A**); 1 mm (**B–K**).

Sponga, 1998) by the distinct pedipalp femoral spine arrangement: femur with 4 dorsal spines (vs. 3 dorsal in *C. camachoi*) and patella with 5 dorsal spines (vs. 4 dorsal spines); differs from *C. bordoni* by retaining well-developed lateral eyes (vs. complete ocular absence in *C. bordoni*); from *C. pardillalensis* by pentasternum shaped like flattened platelets (vs. metasternum granular in shape) and differs from *C. tronchonii* in having fewer anterior carapace setae (6 in *C. santandereanus* vs. more than 6 in *C. tronchonii*) (Fig. 14B) and femur with 4 dorsal spines (vs. 3 dorsal spines).

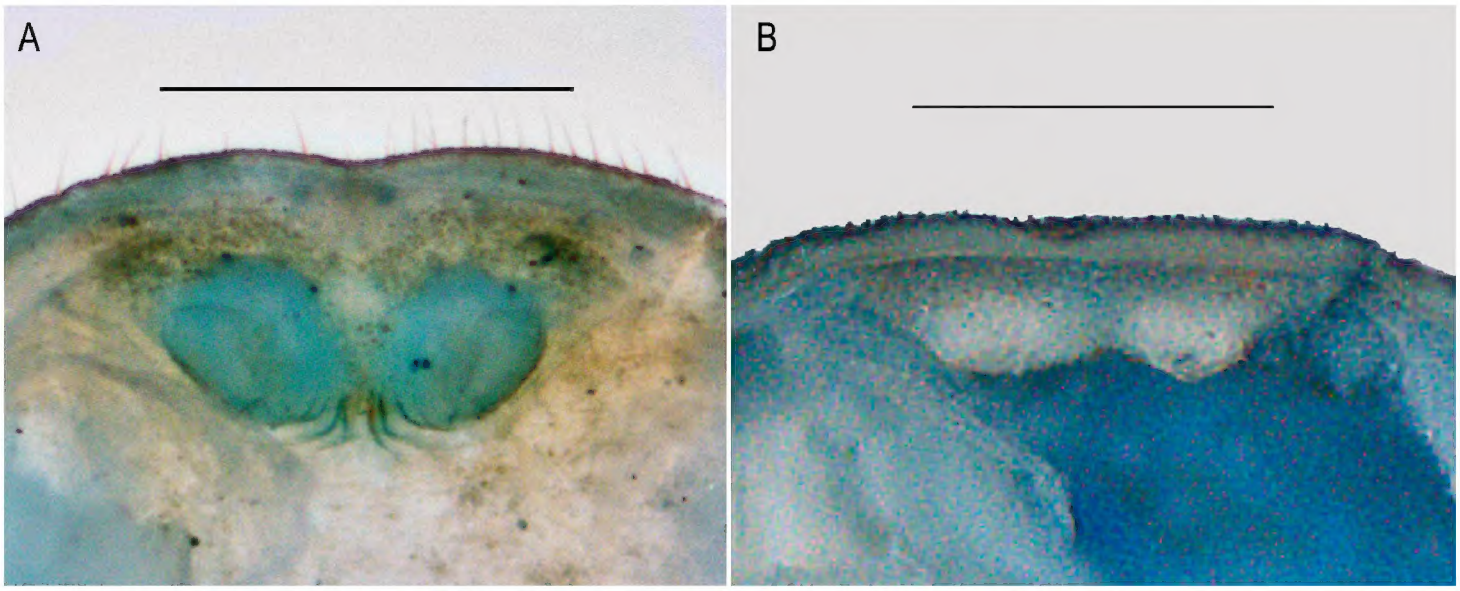

Figure 2. *Charinus santandereanus* sp. nov. (female IAvH). Gonopodes: **A** dorsal view **B** posterior view. Scale bars**:** 0.1 mm.

Etymology. The specific epithet *santandereanus* refers to the type locality, the Department of Santander.

Type material. ***Holotype*** Colombia • ♀; Santander Department; Cueva El Nitro, Villanueva; 06°42'55.2"N, 73°11'47.9"W; altitude 1776 m a.s.l.; 17 Aug. 2024; López, M. F, Lasso C. A. leg. (IAvH-I-7872). ***Paratypes.*** Colombia • 1 ♀, same collection data as for holotype (IAvH-I-7873).

Description. Female. ***Carapace*** (Fig. 1A–C). Frontal process triangular, not visible in dorsal view. Anterior margin straight, with six anterior setae. Median eyes and ocular tubercle absent. Lateral eyes well developed, pale, small seta posterior to each lateral ocular triad. Interocular region finely granulated. ***Sternum*** (Fig. 1D). Tetra-segmented, all platelets markedly sclerotized. Tritosternum projected anteriorly into small, blunt tubercle, surpassing base of pedipalp coxae; medial platelet (tetrasternum) and third platelet (pentasternum) formed by single plates, each with a pair of large anterior setae and several smaller posterior setae; metasternum small, not paired, with pair of small setae, with seven setae in membranous region. ***Opisthosoma.*** Ventral sacs and ventral sac cover absent. ***Genitalia*** (Fig. 2). Female genital operculum with posterior margin slightly convex, with a slight medial indentation, and several setae along margin and on surface. Female gonopods whitish, membranous, cushion-like, with a slightly sclerotized ring-like area and apparently with a circular apical opening on each. With two posteromedial curved and sclerotized ducts. ***Chelicerae*** (Fig. 1E, F). Mesal margin with four teeth: the fourth conspicuously largest, followed by the bifid first tooth, the second, and the third as the smallest. Ectal face with a small, blunt subdistal projection pointing frontally, aligned with the bifid tooth. Claw long, surpassing the fourth basal tooth, with a row of approximately five decreasing teeth. Cusps of the bifid tooth are approximately equal in size. ***Pedipalps*** (Fig. 1G–K). Femur dorsally with two distinct setiferous tubercles proximal to spine 1; primary series with four dorsal spines, decreasing in size from 1 to 4; ventrally with two distinct setiferous tubercles proximal to spine 1,

and primary series with three ventral spines decreasing in size. Patella with four dorsal spines, including a large setiferous tubercle distal to spine I, about one-third length of spine I; two ventral spines the distal larger; setiferous tubercles intercalated between the ventral spines, as well as anterior and posterior to them. Tibia with two dorsal spines, the distal spine twice the length of proximal spine; distal ventral spine on the tibia, with a more developed small setiferous tubercle in basal position, and three distinctive setae between them. Tarsus with two dorsal spines; proximal spine shorter than the distal spine. ***Legs.*** Tibia of leg I with 23 articles; tarsus I with 29 or 30 articles in incomplete legs. None of the specimens have a complete first leg. Leg IV basitibia with two pseudo-articles; trichobothrium bt situated in proximal third, near proximal margin; distal apex of basitibial pseudo-articles with dark, denticulate projection; distitibia trichobothrium bc situated closer to bf than to sbf; sc and sf series each with six trichobothria; tarsus with distinct white annulus distally on first article. ***Measurements.*** See Table 1.

Distribution. Known only from the type locality.

Natural history. This species inhabits a very wet cave. The type specimens were only found in the aphotic zone, on cave walls, close to water. Two other caves in the vicinity, which are hotter and drier, contained no amblypygids.

Remarks. Armas et al. (2012) reported the presence of the genus *Charinus* in Girón, Department of Santander. The record was based on a poorly preserved immature specimen, tentatively identified as "very similar to *Charinus acosta*". Miranda et al. (2021) corrected the coordinates of this record. This is the only previous record of the genus from the department.

Table 1. Measurements (mm) of the body of the female *Charinus santandereanus* sp. nov. (ST-151 c) and male of the *Heterophrynus guacharo*.

Structure	*Charinus santandereanus* sp. nov.	*Heterophrynus guacharo*
Total length	7.97	22.17
Carapace length	2.88	7.54
Carapace width	4.36	12.22
Opisthosoma length	5.09	14.63
Pedipalp – Fe length	2.74	32.32
Pedipalp – Pa length	2.63	33.08
Pedipalp – Ti length	1.46	6.78
Pedipalp – Ta length	1.06	3.76
Pedipalp – Cl length	0.8	
Leg I – Fe Length	9.59	44.94
Leg IV – Fe Length	5.44	25.21
Leg IV – Bt I Length	3.72	17.45
Leg IV – Bt II Length	1.43	3.9
Leg IV – Bt III Length	3.43	7.44
Leg IV – Dt Length	1.64	4.1
Leg IV – Otal	1.05	2.3

Family Paracharontidae Weygoldt, 1996

Jorottui ipuanai Moreno-González, Gutierrez-Estrada & Prendini, 2023

Records. Colombia • ♀; La Guajira Department: Serranía de Bañaderos, upper basin of Camarones River: cave 100 m from Bañaderos Cave, altitude 980 m a.s.l.; La Perrita Cave, 11°00'22"N, 72°55'00.4"W, altitude 968 m a.s.l.; Barrancas, El Vainito Cave, 11°01'04.2"N, 72°54'45.1"W, altitude 998 m a.s.l. (Moreno-González et al. 2023).

Family Phrynidae Blanchard, 1852

Heterophrynus batesii (Butler, 1873)

Figs 3A–F, 4A–D, 15

Material examined. Colombia • ♀ ♂, 1 juv.; Guaviare Department; Cueva Casa de Piedra, Serranía La Macarena/La Lindosa; 02°34'41.52"N, 72°52'21.67"W; altitude 195 m a.s.l. (IAvH-I-7874). Caquetá Department • 2♀, 1♂, 4 juv.; Cueva Necaeridagoda (Cueva de Los Sueños), subcuenca del río Yarí; 02°34'41.52"N, 72°52'21.67"W; altitude 195 m a.s.l.; Carlos A. Lasso leg. (IAvH-I-7875).

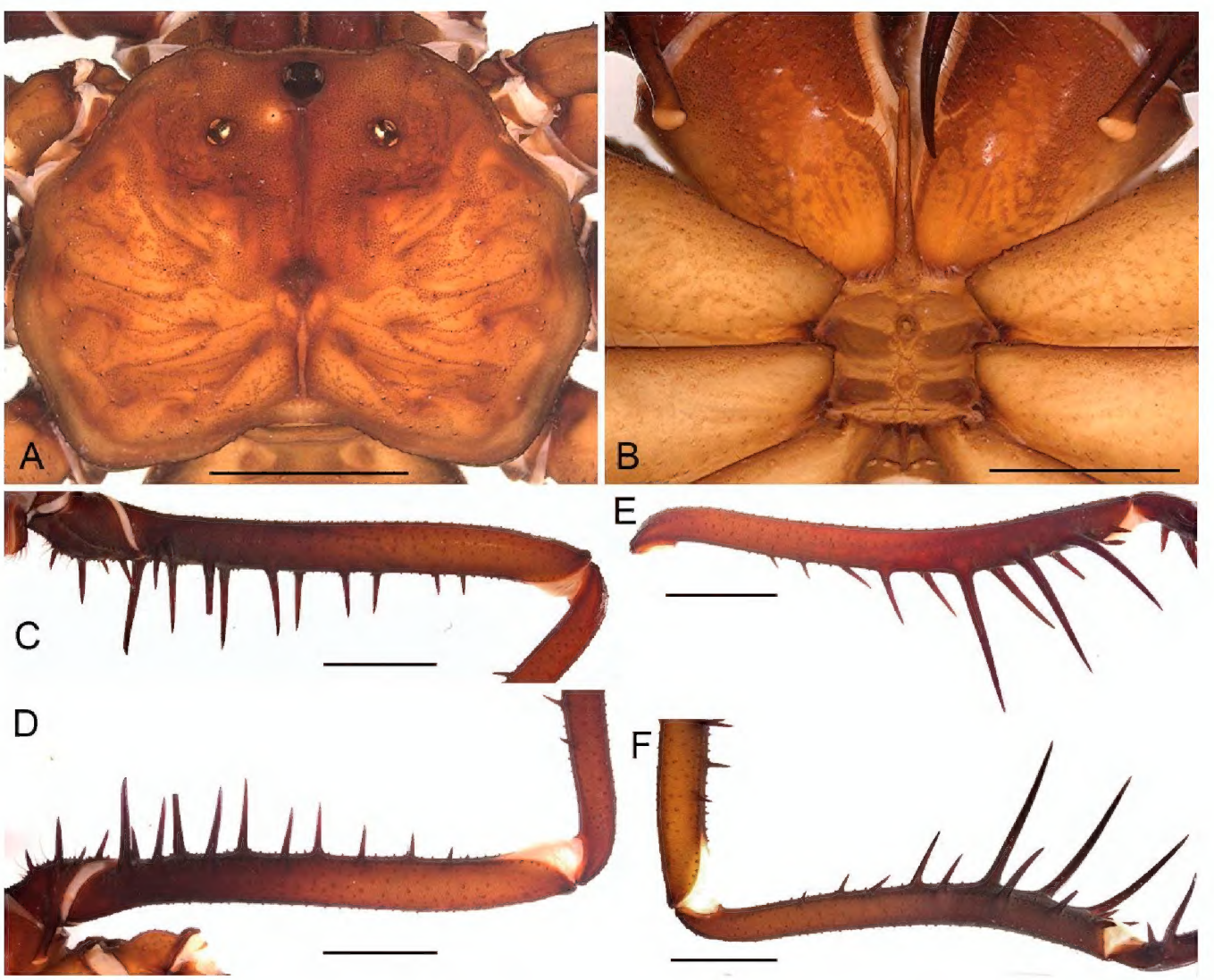

Figure 3. *Heterophrynus batesii*, male from Caquetá (IAvH-I-7875) **A** carapace, dorsal view **B** sternum, ventral view **C, D** Pedipalpal femur, dorsal (**C**) and ventral (**D**) views **E, F** pedipalpal patella, dorsal (**E**) and ventral (**F**) views. Scale bars: 5 mm.

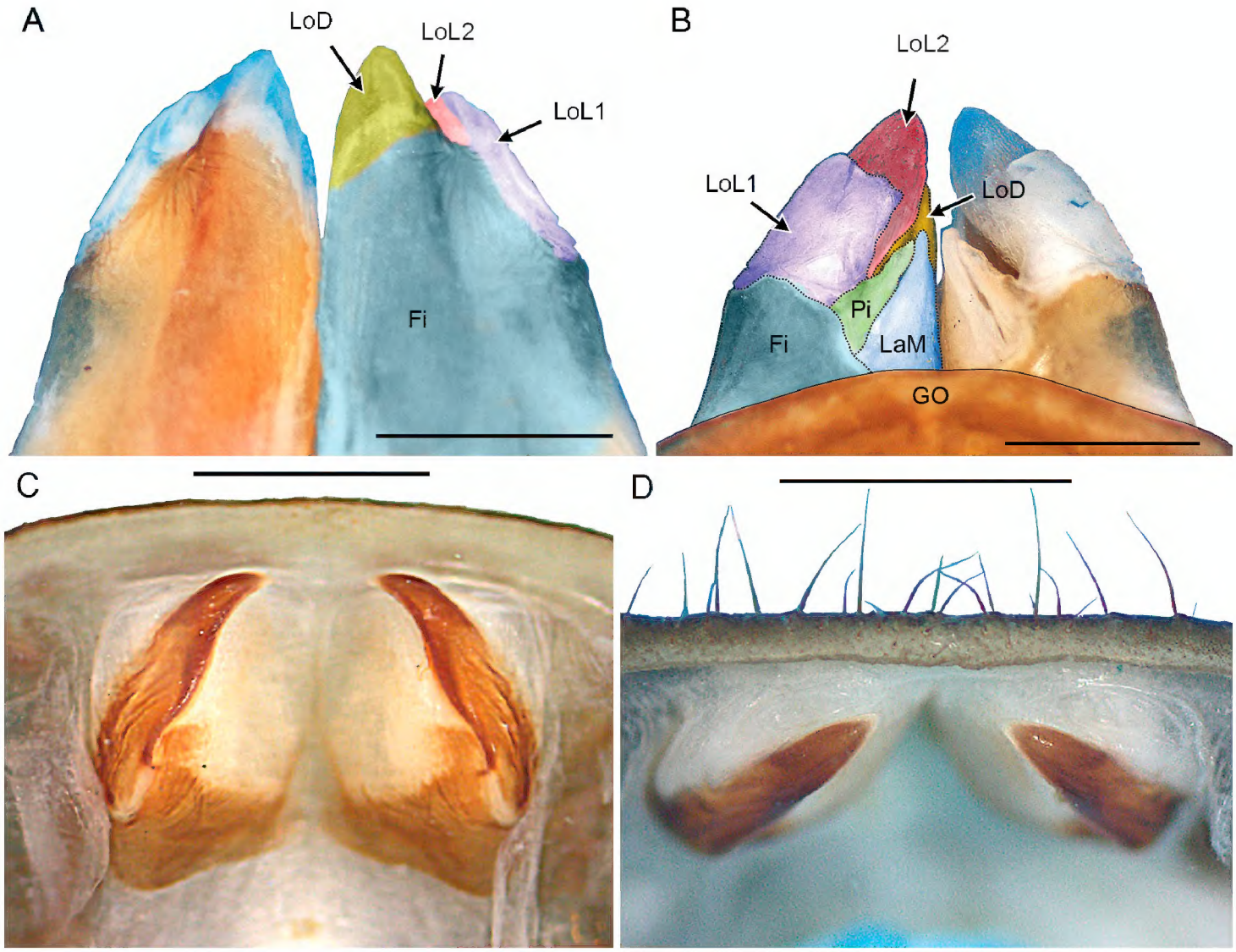

Figure 4. *Heterophrynus batesii* (IAvH-I-7875). Reproductive structures **A, B** Male spermatophore organ, dorsal (**A**) and ventral (**B**) views **C, D** female, gonopods, dorsal (**C**) and posterior (**D**) views **A–D** from SLM-531. Scale bars: 1 mm.

Records. Colombia: Department of Huila, S.O. Acevedo. P.N.N. Cueva de los Guácharos, Cedros sector, Indio Cave; 1850 m a.s.l. (01°36'58.68"N, 76°06'15.12"W) (Víquez et al. 2014).

Remarks. *Heterophrynus batesii* is widely distributed across the Amazon basin, and this record represents its westernmost known occurrence in Colombia, extending its range to the Andean foothills. The species appears to be troglophilic, as supported by previous records from Colombian caves. The morphology of the female gonopods (Fig. 4C, D) largely corresponds to the descriptions and illustrations provided by Giupponi and Kury (2013). Unfortunately, the microsculpture of the male gonopods could not be confirmed due to the lack of SEM images, precluding detailed comparisons of this taxonomically critical feature.

Heterophrynus caribensis **Armas, Torres-Contreras & Álvarez, 2015**
Fig. 15

Records. Colombia: Sucre, Cueva Roca Madre (Armas et al. 2015a).

Heterophrynus cervinus **Pocock, 1894b**
Figs 5A–H, 15

Material examined. Colombia • ♀; Boyaca Department; Caverna Las Cocas; 5°45'84"N, 74°2'21"W; altitude 2000 m a.s.l. Carlos A. Lasso leg. (IAvH-I-7876) (**New departamental record**).

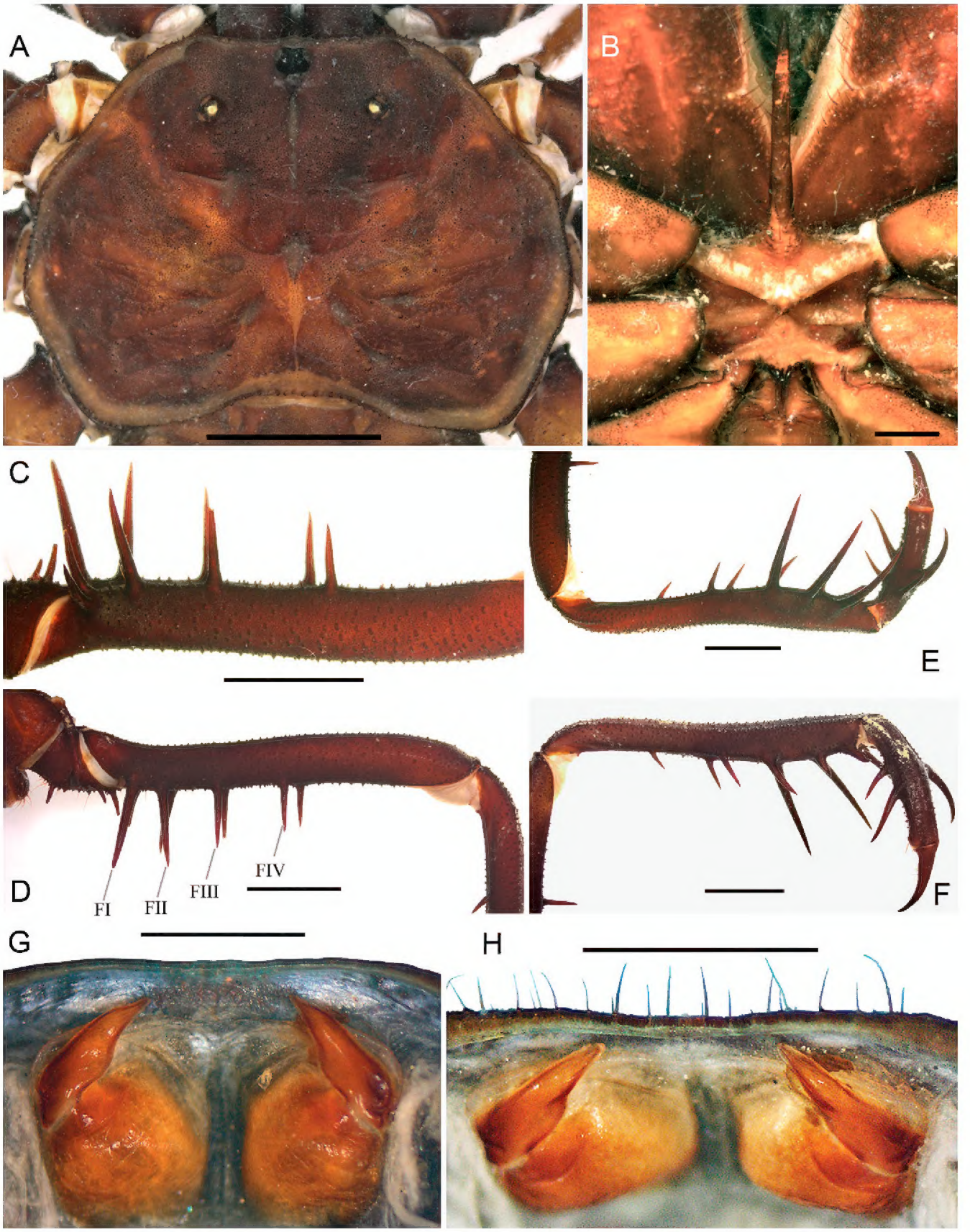

Figure 5. *Heterophrynus cervinus* from Putumayo (IAvH-I-7876) **A** carapace, dorsal view **B** sternum, ventral view **C, D** pedipalpal femur, dorsal (**C**) and ventral (**D**) views **E, F** pedipalpal patella and tibia, dorsal (**E**) an ventral (**F**) views **G, H** female gonopodes, dorsal (**G**) and posterior (**H**) views. Scale bars: 5 mm (**A, C–F**); 1 mm (**B, G, H**).

Records. Colombia: Putumayo, Cavernas de San Carlos (Armas et al. 2015b); Boyaca, Caverna Las Cocas; Tolima, Cunday caves, Tobón; Vereda La Camelia, El Edén cave (Chirivi et al. 2020).

Remarks. The precise type locality of *H. cervinus* remains unknown, and access to the type specimens was unavailable to us. Armas et al. (2015b) reported this species from the Department of Putumayo, and our examination of a single female specimen from a cave in Boyacá reveals morphological concordance with the individuals illustrated by Armas et al. (2015b). However, we observed slight differences, particularly in the gonopod claw, which is more sharply pointed in our specimen, and a more pronounced expansion of the internal lobe—features subtler in the *H. cervinus* illustrated by Armas et al. (2015b). These traits are shared with *H. silviae*, though the latter exhibits clearly curved claws (medially opposed and blunt-tipped). Given these considerations—(1) the lack of access to the type specimens of *H. cervinus*, (2) the uncertainty surrounding the precise type locality, (3) the notable geographical gap between the known Colombian locality for this species and our new record, which approaches the distribution range of *H. silviae*, (4) the absence of male specimens in our material preventing more comprehensive comparisons and (5) the apparent conspecificity between our specimen and those documented by Armas et al. (2015b)—we have tentatively identified our population as *H. cervinus* based on the aforementioned work.

Heterophrynus guacharo Armas, 2015

Figs 6A–D, 7A–F, 15

Material examined. Colombia • ♂; Cueva del Indio, PNN Los Guácharos, cuenca río Suaza (trib. río Magdalena), Huila Department; 01°36'58.4"N, 76°06'16.9"W; altitude 1691 m a.s.l.; Carlos A. Lasso leg. (IAvH-I-7877).

Male gonopodes description (Fig. 7G, H). PI smaller than LaM. LoL1 twice as long as LoL2, with the most distal external portion slightly sculptured. LoL2 striated, visible in both dorsal and ventral views. LoD shorter than LoL1 in dorsal view. Fi clearly chitinized in both views.

Records. Colombia: Huila, Cueva del Indio (Armas 2015).

Remarks. Previously misidentified as *Heterophrynus cervinus* (González and Morales 1986; Morales and González 1986), identification questioned by Armas (2015) and finally described as *H. guacharo* by Armas (2015). The original description of this species included males with dehydrated gonopods, as noted by the original describers ("Both specimens exhibit signs of dehydration, but their overall condition remains good, particularly the holotype") (Armas 2015). Using fresh topotypic material, we provide detailed gonopod illustrations, though SEM data are lacking for microsculpture analysis as presented by Giupponi and Kury (2013). This enables more accurate morphological characterization, overcoming limitations of dehydrated specimens.

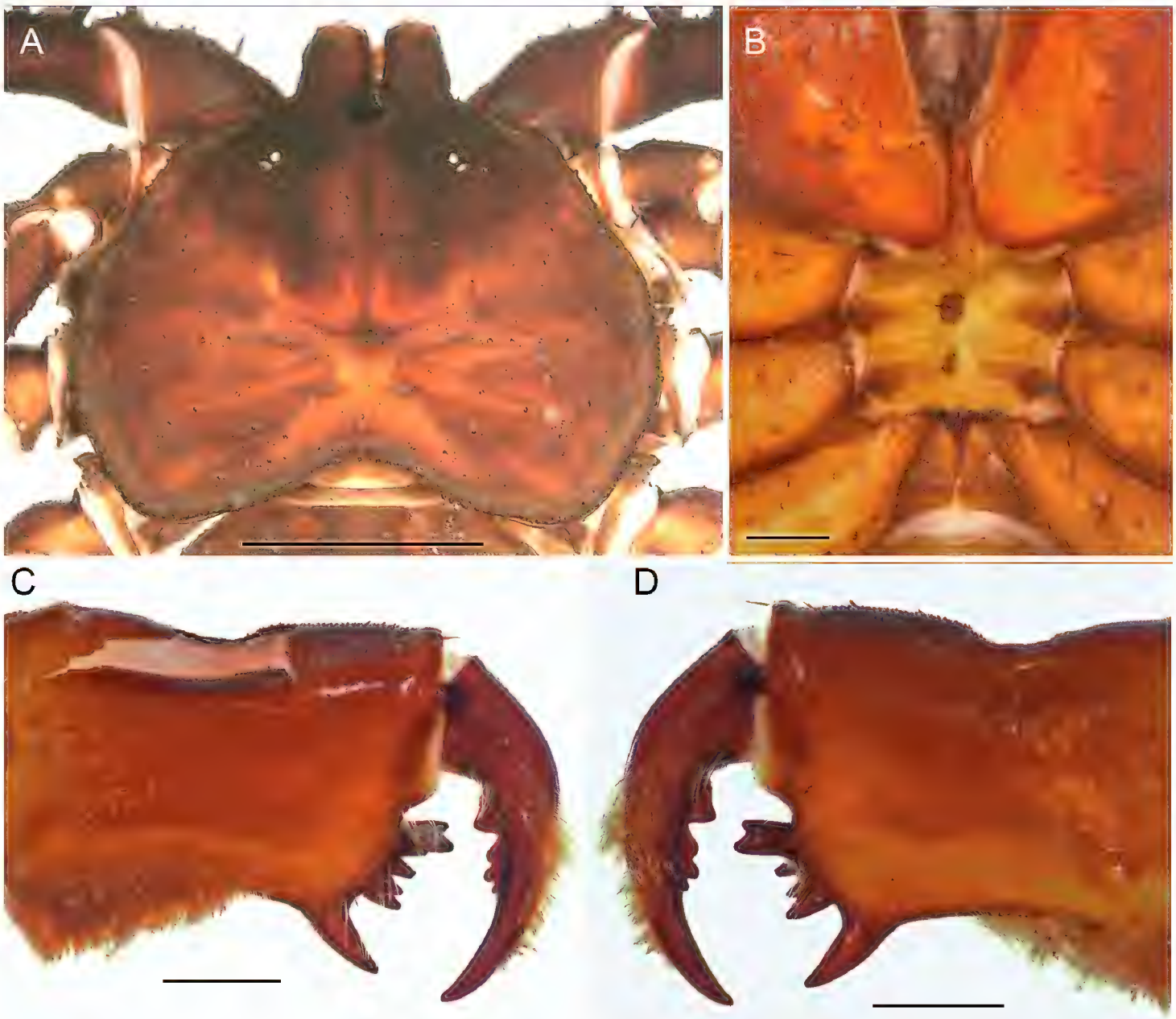

Figure 6. *Heterophrynus guacharo*, male (IAvH-I-7877) **A** carapace, dorsal view **B** sternum, ventral view **C, D** right chelicera, ectal (**C**) and mesal (**D**) views. Scale bars: 5 mm (**A, B**); 1 mm (**C, D**).

Heterophrynus yarigui Álvarez, de Armas & Diaz, 2015

Figs 8A–F, 9A–D, 15

Material examined. Colombia • 2♀ 4♂; Tolima Department; Cueva de Los Guácharos; Cueva el Edén, Municipio Cunday 04°00'42.69"N, 74°45'18.05"W; altitude 840 m a.s.l.; Carlos A. Lasso leg. (IAvH-I-7878) (**New departamental record**).

Remarks. Specimens were collected within a cave, constituting the first troglophilic record for this species, until now known exclusively from epigean habitats (dry forest gullies with rocky substrates and root systems; Armas 2015). Diagnostic characters (pedipalps, gonopods) (Figs 8A–F, 9A–D) match the original description (Armas 2015), showing no troglomorphic adaptations. This demonstrates facultative cave colonization, mirroring ecological plasticity observed in other *Heterophrynus* species.

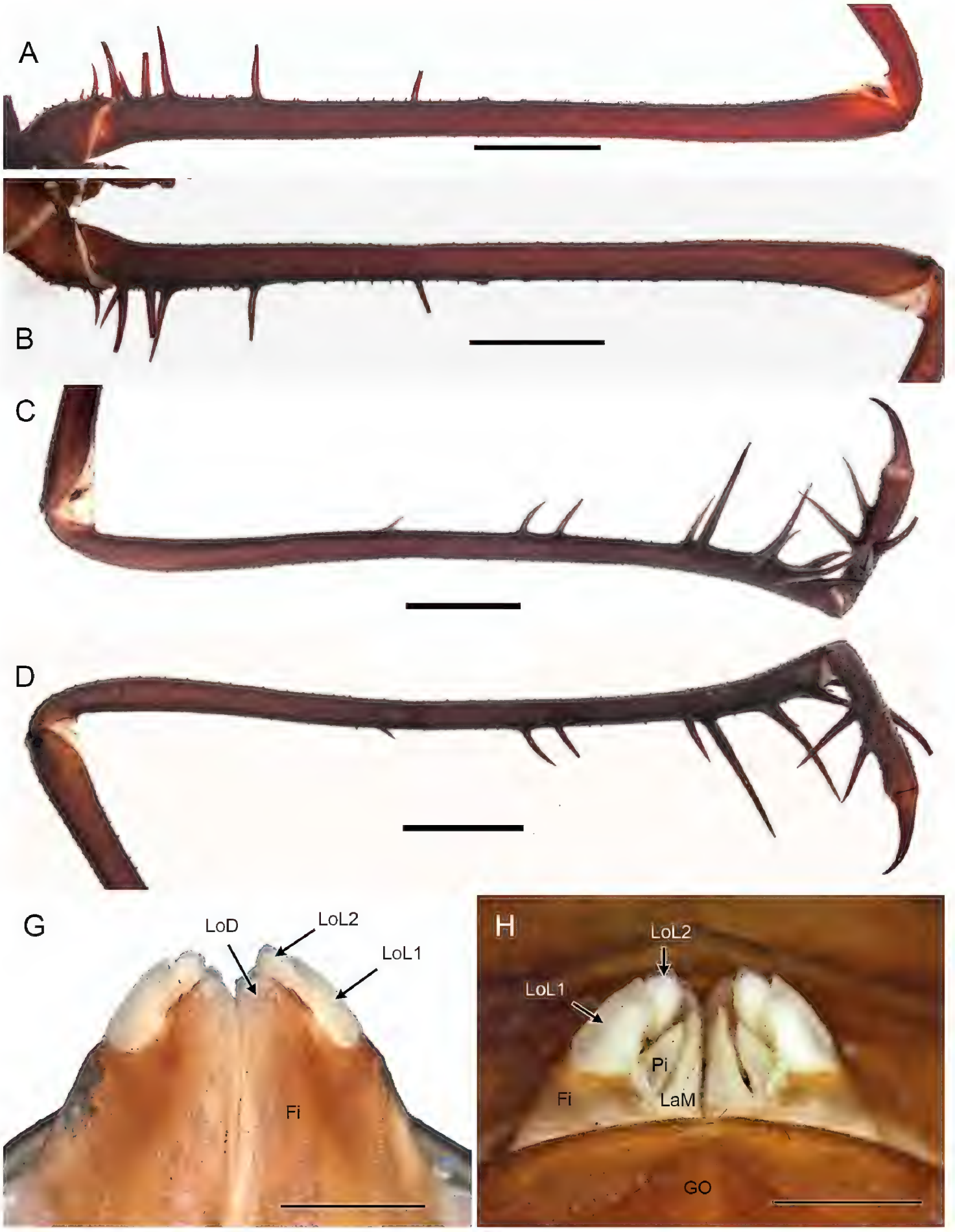

Figure 7. *Heterophrynus guacharo*, male (IAvH-I-7877) **A, B** pedipalpal femur, dorsal (**A**) and ventral (**B**) views **C, D** pedipalpal patella, dorsal (**C**) and ventral (**D**). Reproductive structures: Spermatophore organ, dorsal (**G**) and ventral (**H**) views. Scale bars: 5 mm (**A–D**); 1 mm (**G, H**).

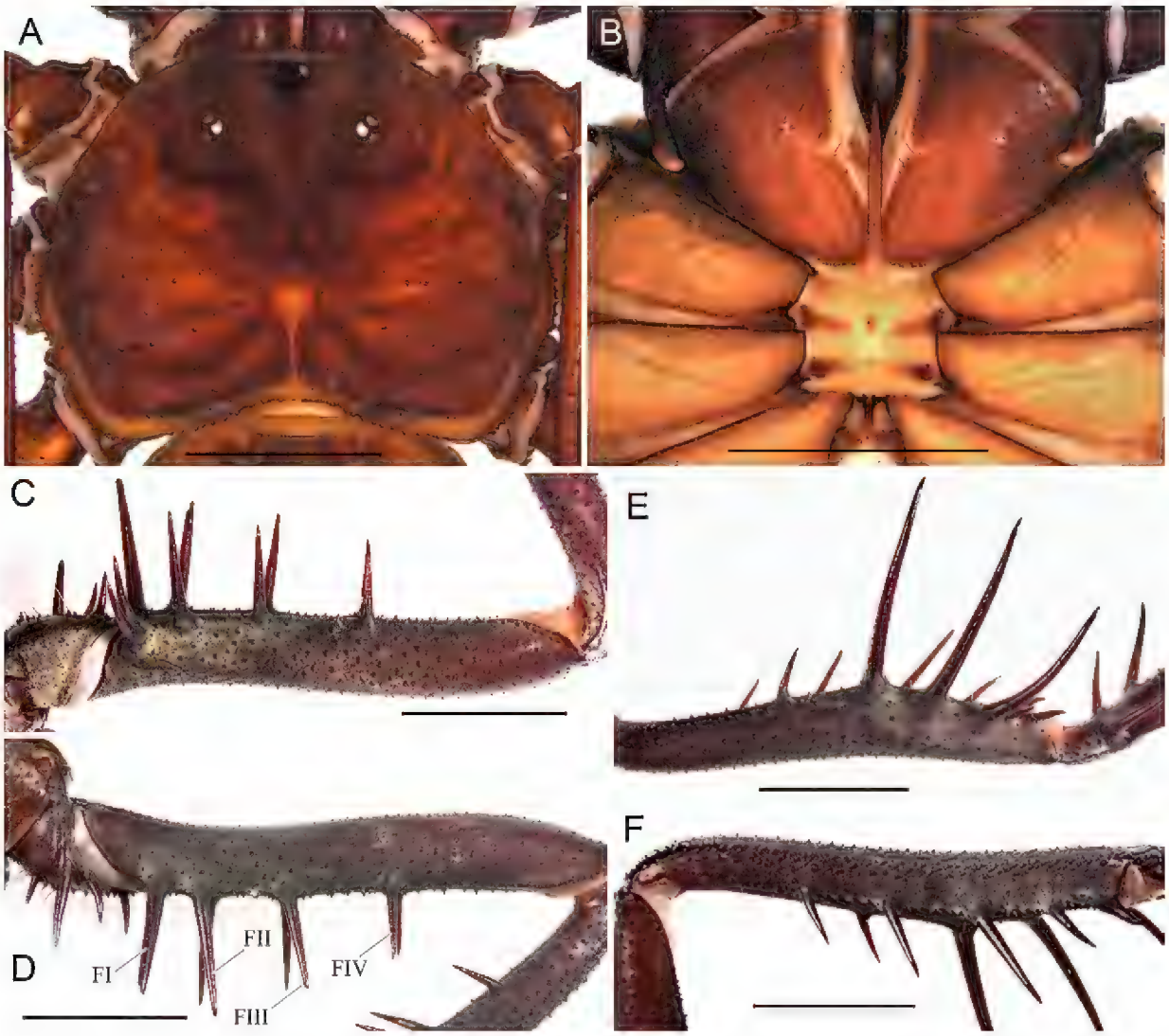

Figure 8. *Heterophrynus yarigui* (IAvH-I-7878) **A** carapace, dorsal view **B** sternum, ventral view **C, D** pedipalpal femur, dorsal (**C**) and ventral (**D**) views **E, F.** pedipalpal patella, dorsal (**E**) and ventral (**F**) views. Scale bars: 5 mm.

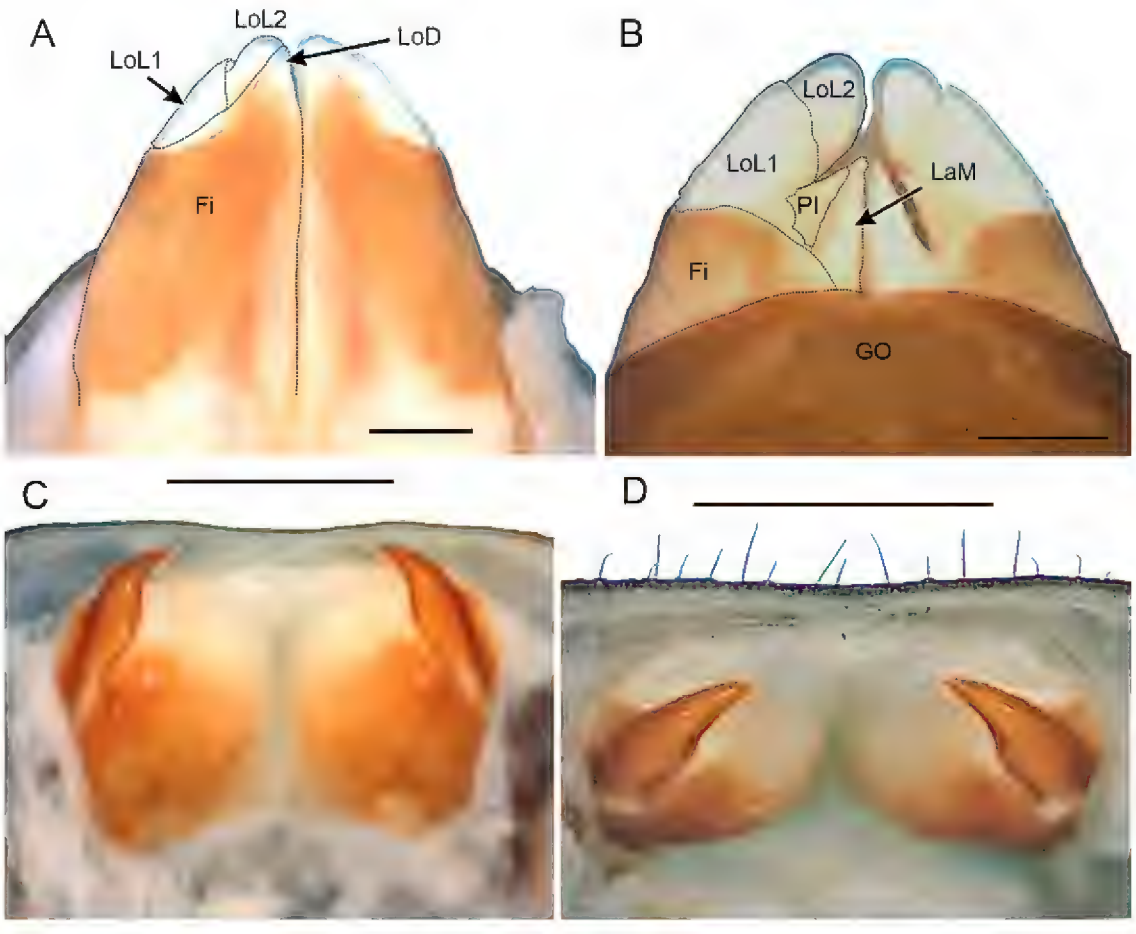

Figure 9. *Heterophrynus yarigui* (IAvH-I-7878). Reproductive structures **A, B** male spermatophore organ, dorsal (**A**) and ventral (**B**) views **C, D** female, gonopods, dorsal (**C**), and posterior (**D**) views. Scale bars: 1 mm.

Paraphrynus laevifrons **(Pocock, 1894b)**
Figs 10A–F, 11A–D, 15

Material examined. Colombia • 1♀ 1♂; Providencia Island; Represa túnel artificial; Freshwater Bay, Isla de Providencia, Archipiélago de San Andrés, Providencia y Santa Catalina; 12°20'38.4"N, 81°23'16.9"W; 0 m a.s.l.; Carlos A. Lasso leg. (IAvH-I-7879) (**New record**). • 1♀ 1♂; Cueva Bat Hole, Chay Hill, Isla de Providencia, Archipiélago de San Andrés, Providencia y Santa Catalina; 13°20'20"N, 81°23'44.8"W; 0 m a.s.l.; Carlos A. Lasso leg. (PV-39) (**New record**). • ♀♂; Cueva de Sara, Isla de San Andrés, Archipiélago de San Andrés, Providencia y Santa Catalina; 12°32'41.4"N, 81°43'37.8"W; 0 m a.s.l.; Carlos A. Lasso leg. (IAvH-I-7881).

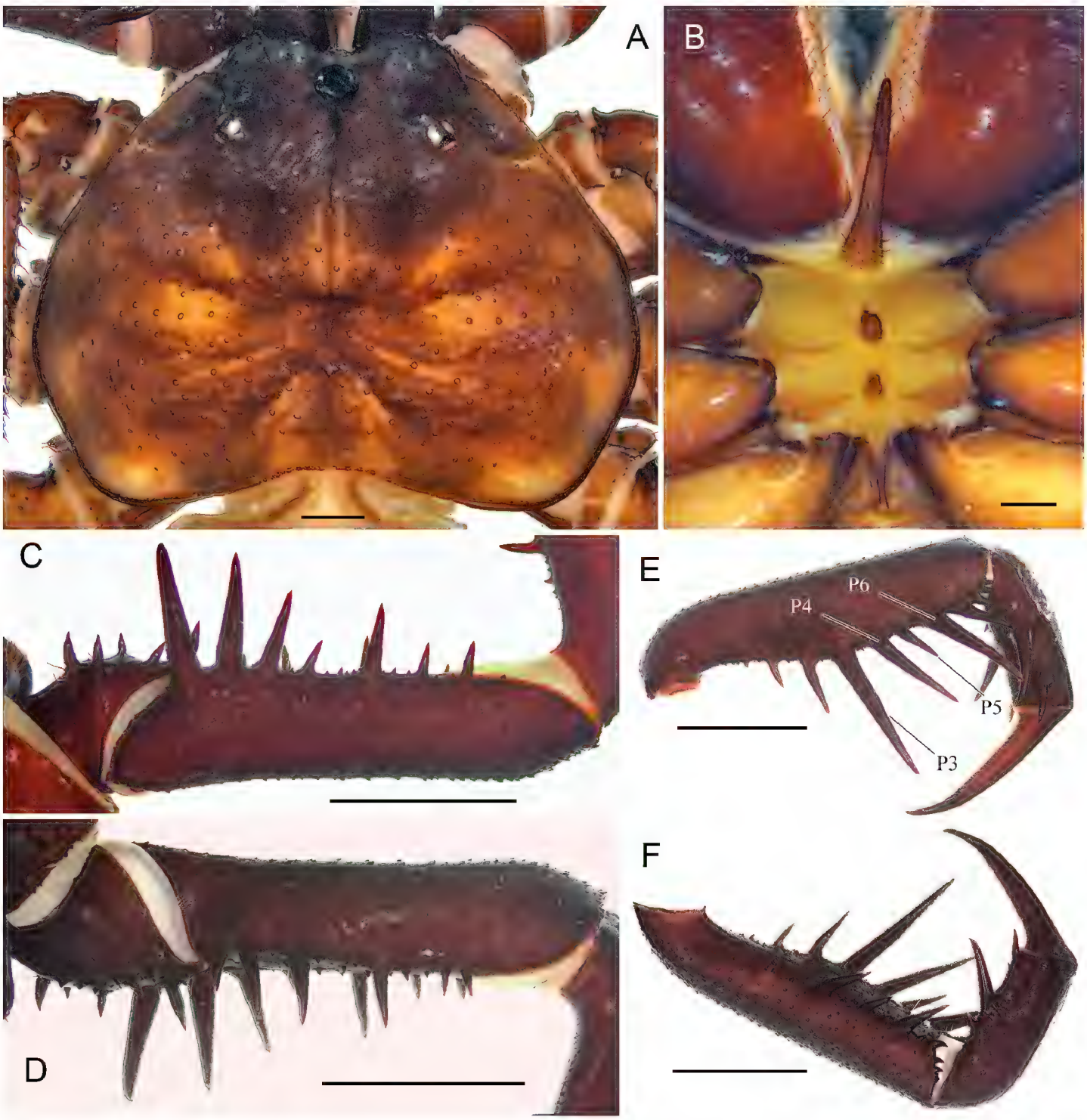

Figure 10. *Paraphrynus laevifrons* from Provendicia Island (IAvH-I-7880) **A** carapace, dorsal view **B** sternum, ventral view **C, D** pedipalpal femur, dorsal (**C**) and ventral (**D**) views **E, F** pedipalpal patella, dorsal (**E**) and ventral (**F**) views **G, H** male spermatophore organ, dorsal (**G**) and ventral (**H**) views **I, J** female gonopodes, dorsal (**I**) and posterior (**J**) views. Scale bars: 1 mm (**A, B**); 5 mm (**C–F**).

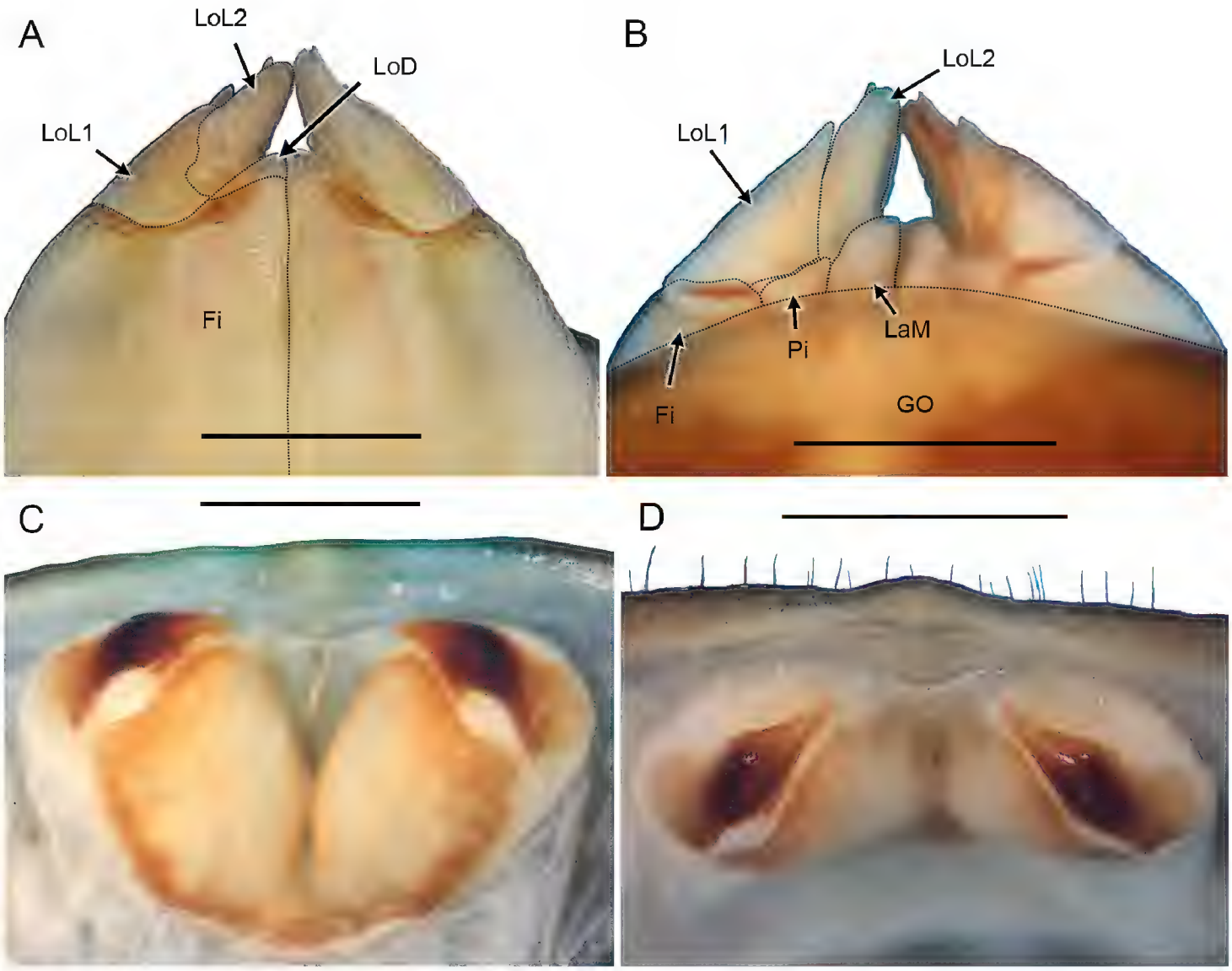

Figure 11. *Paraphrynus laevifrons* (IAvH-I-7880). Reproductive structures **A, B** male spermatophore organ, dorsal (**A**) and ventral (**B**) views **C, D** female, gonopods, dorsal (**C**), and posterior (**D**) views. Scale bars: 1 mm.

Records. Colombia, San Andrés (Chirivi and Armas 2012); Providencia; Chocó (Chirivi and Armas 2012).

Remarks. *Paraphrynus laevifrons* is a species with a wide distribution in Central and North America, including the Yucatán Peninsula, where it inhabits various environments, including caves (Reddell 1981; Chirivi and Armas 2012). The species lacks a precise type locality, being broadly described from "West coastal America." In Colombia, it has only been recorded from two localities—Isla San Andrés and Chocó (Chirivi and Armas 2012). Our study provides the first record of this species from Providencia Island (Caribbean Sea), as well as the first record of *P. laevifrons* in a cave habitat in Colombia. Due to (1) the absence of a specific type locality, (2) the lack of direct examination of the holotype, and (3) the morphological similarity of our specimens with those described by Chirivi and Armas (2012), we have followed their identification to designate the specimens from Providencia studied here. It is noteworthy, however, that the material identified as *Paraphrynus laevifrons* from Guatemala by (Armas et al. 2017) shows significant differences, casting doubt on the conspecificity of these populations. Integrative systematics studies reveal a cryptic diversity in some populations from Southwestern North America (Cazzaniga and Prendini 2024).

Natural history. The specimens from Providencia Island were collected from a cave located along the coast, with the upper section consisting of sand and dry guano, while the lower section is inundated with seawater and subjected to wave action. The cave is situated approximately 10 meters from the shoreline, exposed to the effects of wave impact. The adaptation of these species to such conditions remains unclear.

Phrynus araya Colmenares & Villarreal, 2008

Figs 12A–F, 13A–D, 14B, 15

Material examined. Colombia • ♀, 1 juv.; Santander Department; (IAvH-I-7882) Cueva del Nitro, Municipio La Aguada; 06°10'32"N, 73°30'52.3"W; (ST-183d) (New record) • Cueva La Catedral, Municipio La Aguada, Santander; 06°11'0.5"N, 73°31'7.1"W; altitude 1789 m a.s.l.; Carlos A. Lasso leg. (IAvH-I-7883) (**New cave record**).

Records. Colombia: Santander, Cueva del Muerto, Cueva del Nitro (Chirivi and Armas 2012), Cueva La Catedral.

Remarks. Originally described from Venezuela and recorded from Colombia by Chirivi and Armas (2012).

Phrynus pulchripes (Pocock, 1894a)

Records. Colombia: Santander Departament: Cueva El Rascadero, Villanueva (7°26'56"N, 73°15'14"W): (ICN-AM 85), Cueva del Nitro, vereda Agua Fría; 6°40'4.99"N, -73°10'39.99"W; (Chirivi 2017).

Remarks. It is worth noting that a previous record from the same cave, documenting *Phrynus araya*, was made by Chirivi and Armas (2012). It would be interesting to verify whether sympatry occurs between the two species or if a misidentification might have occurred in either of the two instances.

Key to cave-associated amblypygids species in Colombia

1 Articulation of the pedipalp parallel to the body axis; anteromedial portion of carapace slightly projected forward (Moreno González 2023: fig. 5A) .... ***Jorottui ipuanai* (Paracharontidae)**

– Pedipalp articulation oblique or perpendicular to body axis (Fig. 14A–C); anteromedial portion of carapace not projected forward (Figs 1B, 3A) .... **2 (Charontidae, Phrynidae)**

2 Body small (carapace length <3 mm, width <4 mm). Tarsus of walking leg with arolium (Torres et al. 2019: fig. 3F) ..... **3 (Charontidae)**

– Body larger (carapace length >15 mm, width >20 mm). Tarsus of walking leg without arolium ..... **6 (Phrynidae)**

3 Median eyes present but reduced (Miranda et al. 2021: fig. 24C) .... ***Charinus miskito***

– Median eyes absent (Fig. 1B, C)..... **4**

4 Leg IV basitibia with three pseudo-articles ..... ***Charinus rocamadre***

– Leg IV basitibia with two pseudo-articles **5**

5 First cheliceral tooth bicuspid with two subequal denticles; dorsal margin of tooth concave (Fig. 1E, F); pentasternum with paired setae inserted on a single, shared sclerotized base (Fig. 1D) ..... ***Charinus santandereanus* sp. nov.**

– First cheliceral tooth bicuspid with dorsal denticle distinctly smaller (Miranda et al. 2021: fig. 10E, F); dorsal margin of tooth straight; pentasternum with paired setae each on independent sclerotized bases (Miranda et al. 2021: fig. 42B) ..... ***Charinus mocoa***

6 Pedipalpal trochanter with retroposterior apophysis (Fig. 3D; Quintero 1981: fig. 11) .....7 (***Heterophrynus***)

– Pedipalpal trochanter lacking retroposterior apophysis (Fig. 10D)..... **11**

7 Pedipalpal femur with ventral spines FII shorter than FI and FIII (Fig. 3D)..... **8**

– Pedipalpal femur with ventral spines FII longer than FI and FIII (Fig. 7B) **9**

8 External ventral teeth of the basal segment of the chelicera tricuspid (Armas et al. 2015: fig. 1G)..... ***Heterophrynus caribensis***

– External ventral teeth of the basal segment of the chelicera bicuspid (Fig. 6C, D).....***Heterophrynus batesii***

9 Femur pedipalpal with five ventral spines; female gonopods strongly curved, pointing inward or posteriorly, with blunt tips and no internal medial expansion (Armas 2015: fig. 1C).....***Heterophrynus guacharo***

– Femur pedipalpal with four ventral spines (Fig. 5C, D, 8C, D); female gonopods gently curved inward, with pointed tips and with internal medial expansion (Figs 5G, H, 9C, D) **10**

10 Female gonopod with distal third of sclerite narrow and straight, mostly smooth, lacking dorsal depressions (Fig. 5G, H) ....***Heterophrynus cervinus***

– Female gonopod basally widened and distally curved, bearing two conspicuous longitudinal dorsal depressions (sometimes fused into one) (Álvarez et al. 2015: figs 1F, 2A); external lateral surface with a groove or striation extending to midlength of gonopod (Fig. 9C, D).....***Heterophrynus yarigui***

11 With two small spines between Pd3 and Pd5 (Fig. 10E) ....***Paraphrynus laevifrons***

– With single small spine between Pd3 and Pd5 (Fig. 12E)..... **12** (***Phrynus***)

12 Pd5 larger than Pd2 and Pd3 (Chiriví 2017: fig. 6B). Female gonopods thick and curved (Chirivi 2017: fig. 1B) ..... ***Phrynus pulchripes***

– Pd5 shorter than Pd2 and Pd3 (Fig. 12E, F). Female gonopods slender and elongated (Colmenares and Villarreal 2008: fig. 8, Chiriví and Armas 2012: fig. 3D).....***Phrynus araya***

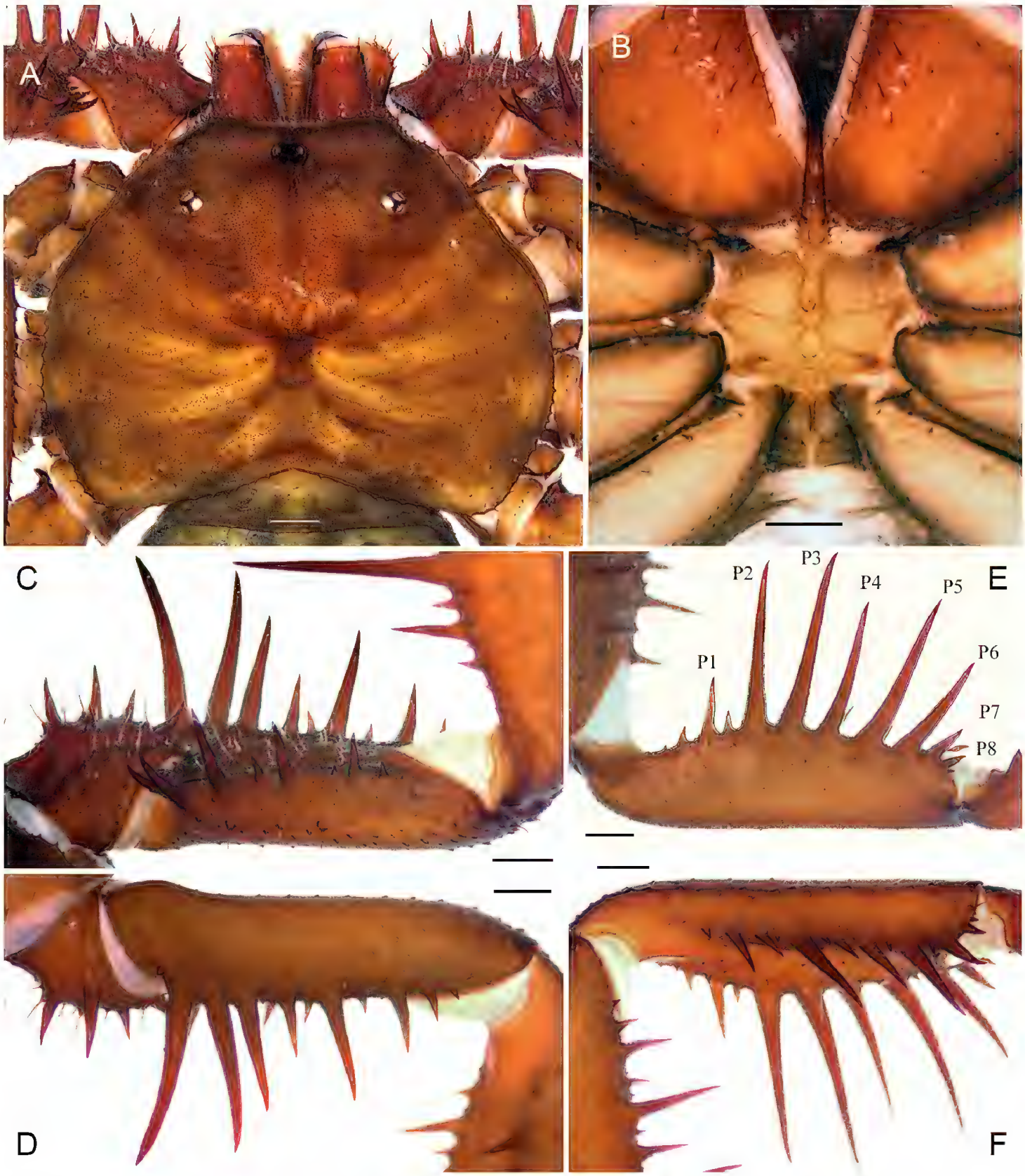

Figure 12. *Phrynus araya*, female from Santander (IAvH-I-7883) **A** carapace, dorsal view **B** sternum, ventral view **C, D** pedipalpal femur, dorsal (**C**) and ventral (**D**) views **E, F** pedipalpal patella, dorsal (**E**) and ventral (**F**) views. Scale bars: 1 mm.

Synthesis of results A total of 53 specimens of amblypygids from 12 Colombian caves in eight departments were examined (Table 2), representing four genera and seven species. *Charinus* is represented by an undescribed species, here named *C. santandereanus* sp. nov. The genus *Heterophrynus* is recorded for the first time in six caves across the departments of Guaviare (Serranía La Macarena/La Lindosa), Antioquia, Caquetá, and Boyacá. The previously unknown male gonopods of *H. guacharo* are described, using

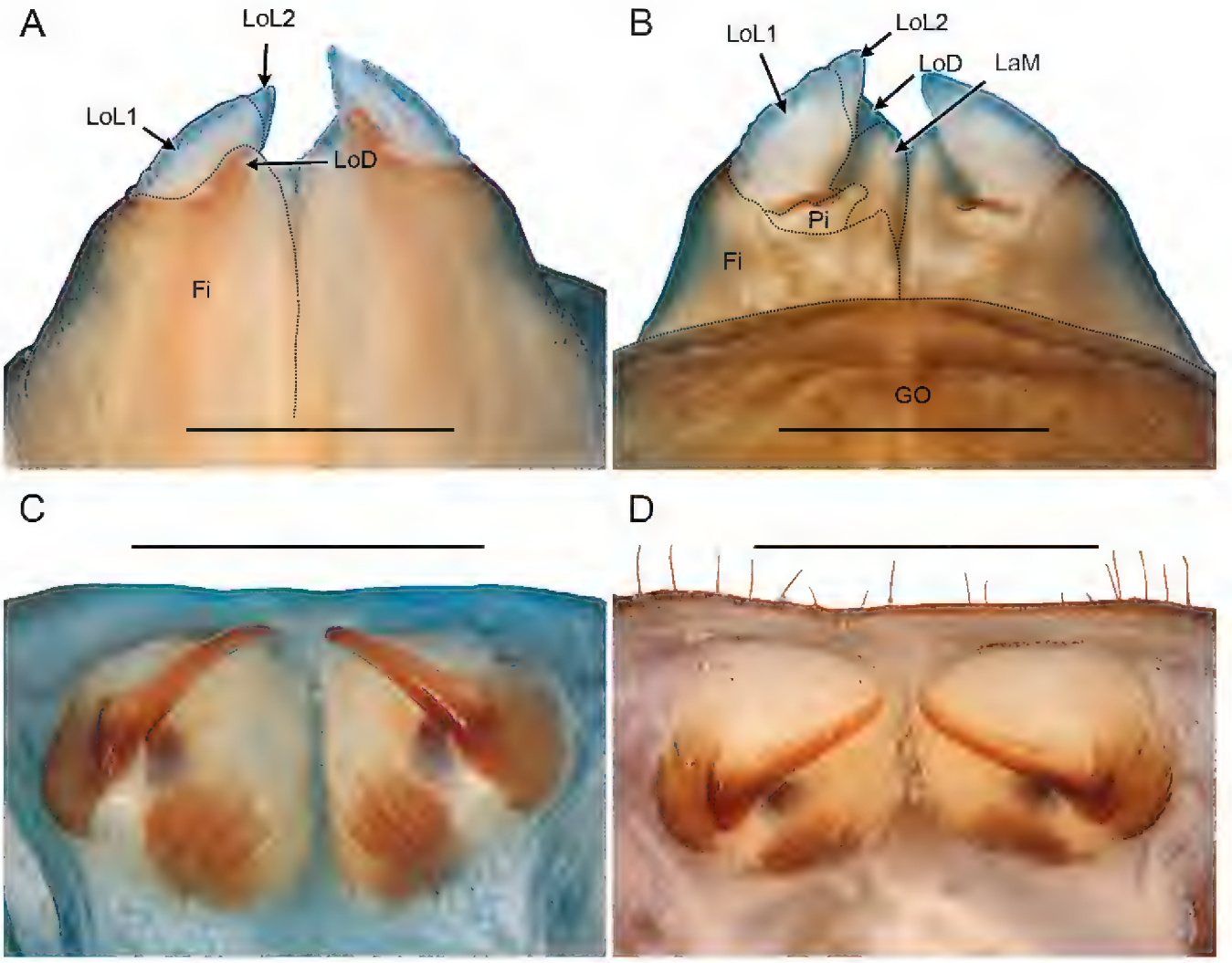

Figure 13. *Phrynus araya* (IAvH-I-7883). Reproductive structures **A, B** male spermatophore organ, dorsal (**A**) and ventral (**B**) views **C, D** female, gonopods, dorsal (**C**), and posterior (**D**) views. Scale bars: 1 mm.

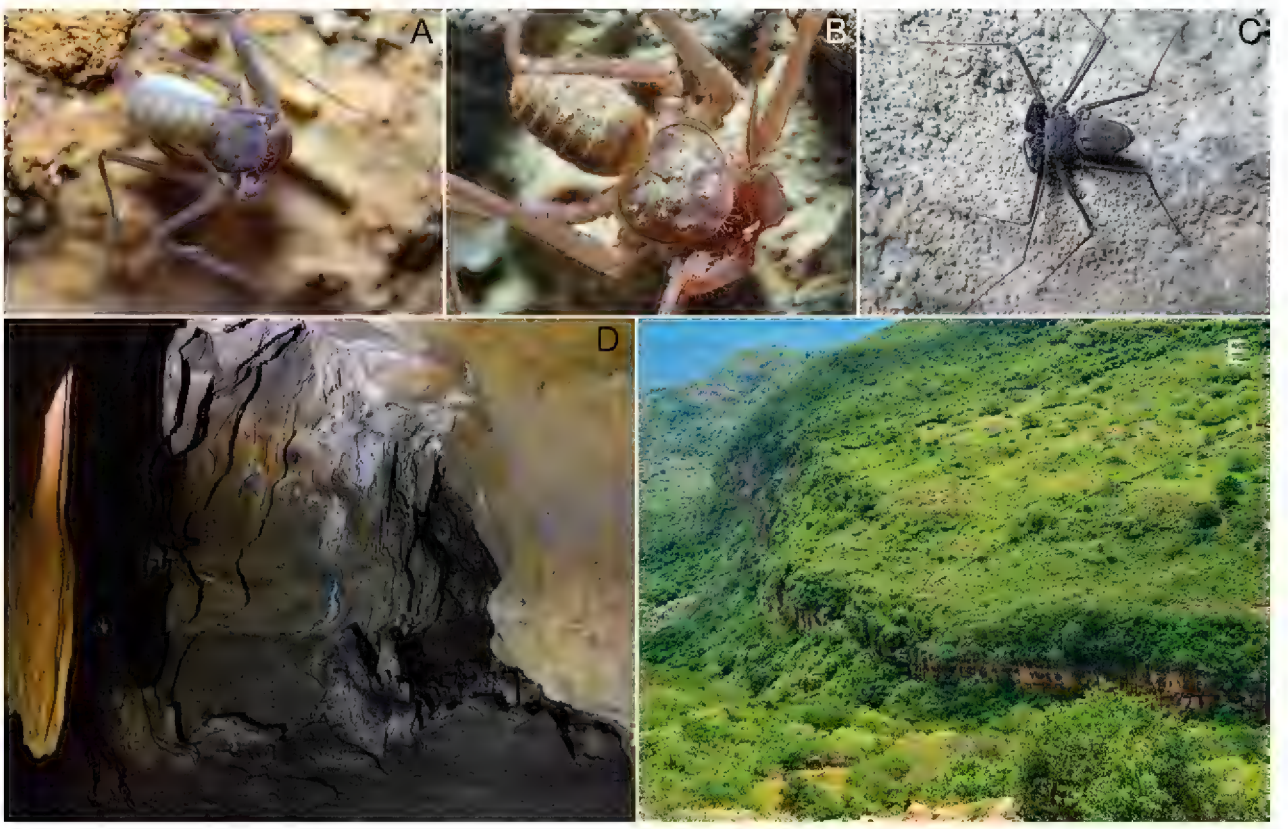

Figure 14. A *Charinus santandereanus* sp. nov., from department of Santander, Cueva el Nitro Villanueva, Santander **B** *Charinus tronchonii* (Ravelo, 1977), from Cueva del Cuarzo, Falcón, Venezuela. *Phrynus araya* Colmenares & Villarreal, 2008, from department of Santander, Cueva Fumador **D, E** Cueva del Nitro, Santander, views of the cave interior (**D**) and the rocky outcrop housing the cave entrance (**E**). Photos: **A, C** Manuel F. López, **B** Osvaldo Villarreal **D, E** Gonzalo Valdivieso.

Table 2. List of caves evaluated by department and the species of amblypygids found.

Departament	Cave	Longitude, Latitude	Altitude	Species
Antioquia	Caverna Los Guácharos, Reserva Río Claro, Río Claro (cañón)	5°49'43.1"N, 74°49'55.3"W	390	*Heterophrynus* sp.
Boyacá	Cueva Las Cocas	5°46'24"N, 74°2'20.9"W	2000	*Heterophrynus cervinus*
Caquetá	Cueva Necaeridagoda (cueva de Los Sueños), subcuenca del río Yarí, Caquetá	0°10'46.3"N, 72°32'31.9"W	173	*Heterophrynus batesii*
Santander	Cueva La Catedral, Municipio La Aguada, Santander	6°11'0.5"N, 73°31'7.1"W	1793	*Phrynus araya*
	Cueva El Nitro, Villanueva, Santander	6°42'55.2"N, 73°11'47.9"W	1776	*Charinus santandereanus* sp. nov.
	Cueva El Nitro, Municipio La Aguada, Santander	6°10'32"N, 73°30'52.3"W	1789	*Phrynus araya*
Tolima	Cueva de Los Guácharos, Cunday, Tolima	4°0'42.7"N, 74°45'18.05"W	840	*Heterophrynus yarigui*
Guaviare	Casa de Piedra, abrigo rocoso río Guayabero, Serranía La Macarena, Guaviare	2°34'41.5"N, 72°52'21.7"W	195	*Heterophrynus batesii*
Huila	Cueva del Indio, PNN Los Guácharos, cuenca río Suaza (afl. río Magdalena), Andes, Huila	1°36'58.4"N, 76°6'16.9"W	1691	*Heterophrynus guacharo*
San Andrés y Providencia	Cueva Bat Hole, Chay Hill, Isla de Providencia, Archipiélago de San Andrés, Providencia y Santa Catalina	13°20'20"N, 81°23'44.8"W	0	*Paraphrynus laevifrons*
	Cueva de Sara, Isla de San Andrés, Archipiélago de San Andrés, Providencia y Santa Catalina	12°32'41.4"N, 81°44'37.9"W	0	*Paraphrynus laevifrons*
	Represa Freshwater Bay, Isla de Providencia, Archipiélago de San Andrés, Providencia y Santa Catalina	12°20'38.4"N, 81°23'16.9"W	0	*Paraphrynus laevifrons*

topotypic specimens. The genus *Paraphrynus*, with a single species previously known from Colombia, *P. laevifrons* (Chiriví and Armas 2012) recorded from San Andrés Island and Chocó, is reported for the first time in hypogean environments in the country.

Discussion

Our results provide new knowledge on cave-dwelling amblypygids in Colombia, including the description of a new species. The association of Amblypigi with caves in Colombia has been documented in three families and five genera. The monotypic *Jorottui*, the sole representative of the family Paracharontidae in the New World, may represent a faunal relict of this group (Moreno-González et al. 2023; Miranda et al. 2024). The family Charontidae is represented by the diverse genus *Charinus*, with species frequently associated with caves (Miranda et al. 2021), including some troglobitic representatives. Some species lack median eyes, a feature shared by the newly described species *C. santandereanus* sp. nov. and some geographically nearby cave-dwelling species such as *C. rocamadre*, *C. tronchonii* (Ravelo, 1975), and *C. bordoni*

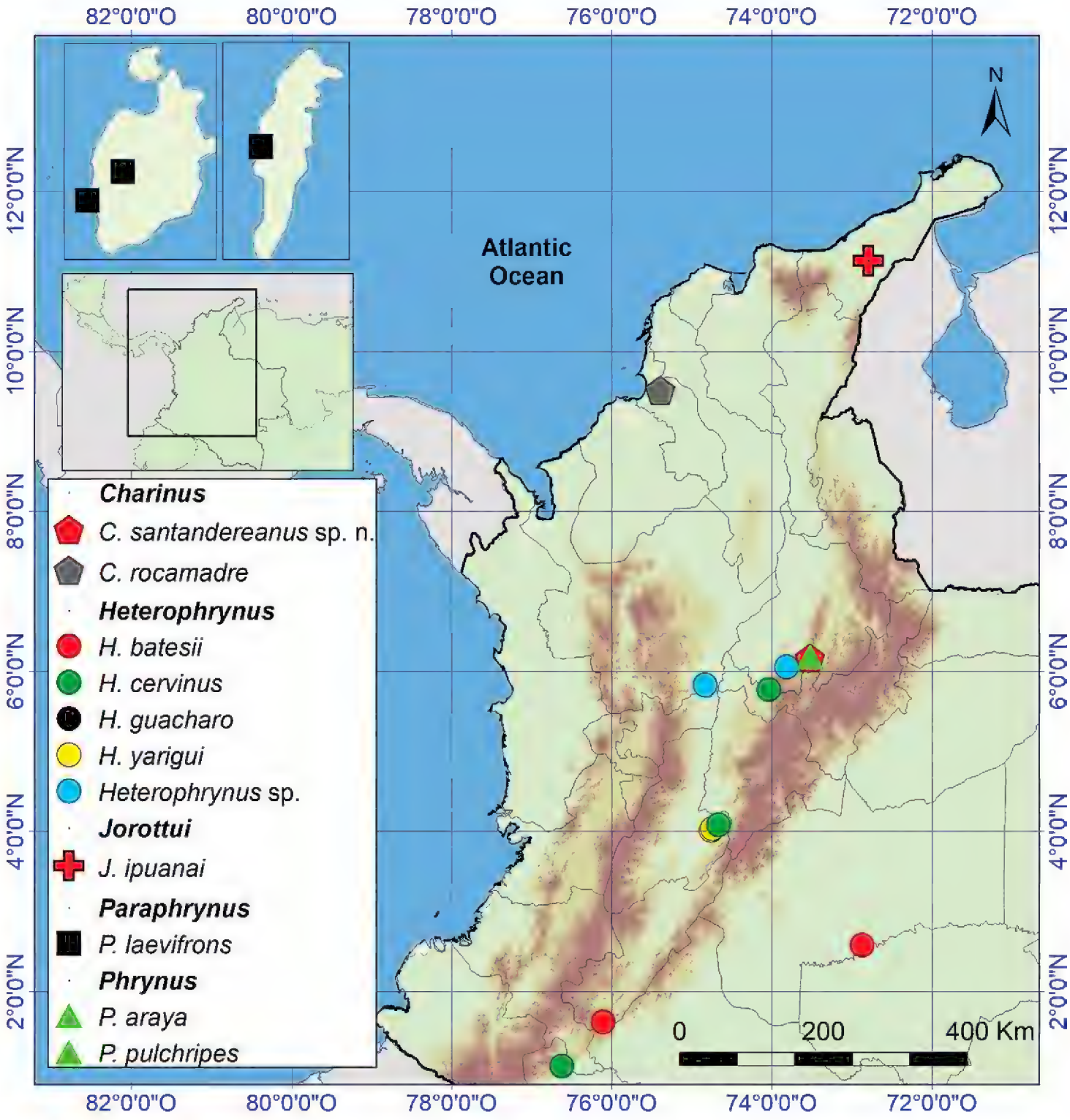

Figure 15. Map showing the records of Amblypygi associated with Colombian caves.

(Ravelo 1977) (Ravelo 1975; Ravelo 1977). Phrynidae being the family most widely represented and known, it is also the most abundant in the Colombian cave fauna, with three genera: *Paraphrynus* (1 sp.), *Phrynus* (2 spp.), and *Heterophrynus* (5 spp.). A record of this genus was presented by Barriga et al. (2019) for a cave in Santander, but it was not identified to the species level. *Paraphrynus* is a common representative of the fauna in Central and North America, and parts of the Caribbean, particularly in the Greater Antilles. However, *Paraphrynus* is present in Colombia in Chocó, and on insular land, specifically in the islands of the San Andrés-Providencia Archipelago, located approximately 750 km north of the Colombian mainland.

The identification and first description of the male genital of the *Heterophrynus guacharo* from PNN Los Guácharos provides morphological data, enabling

comparisons with other species in the genus and clarifying their taxonomic relationships. Additionally, the discovery of *Heterophrynus batesii*, *H. cervinus*, and *H. yarigui* in hypogean environments expands our understanding of their distribution and suggests their ability to exploit subterranean habitats, though further studies are needed to determine their ecological role in these systems. In Colombia, the cavernicolous fauna of Amblypygi predominantly represented by the genus *Heterophrynus*, in contrast to other South American countries where the genus *Charinus* is commonly associated with cave and hypogean environments (e.g., Ravelo 1977; Giupponi and Miranda 2016; Barriga et al. 2019; Miranda et al. 2021). In Colombia, *Charinus* has been recorded in only one cave in the Caribbean, where *C. rocamadre* occurs sympatrically with *Heterophrynus caribensis* (Torres-Contreras et al. 2015).

While this study does not establish definitive distribution patterns, we document species occurrences and provides morphological data for cave-dwelling amblypygids in Colombia. Our records of *Heterophrynus guacharo*, *H. batesii*, *H. cervinus* and *H. yarigui* reveal or ratifies their presence in hypogean environments, though the absence of troglomorphic traits suggests opportunistic rather than obligatory cave use. While this study does not assess ecological interactions or conservation implications, it establishes baseline distribution patterns that differ from *Charinus*-dominated cave faunas reported elsewhere in South America (Baptista and Giupponi 2002; Vasconcelos and Ferreira 2017), the apparent dominance of *Heterophrynus* in Colombian caves requires cautious interpretation—this pattern could reflect sampling artifacts favoring larger amblypygids, a true biogeographical segregation, or undetected microhabitat partitioning with smaller taxa.

These findings underscore the importance of standardized cross-regional sampling to differentiate ecological patterns from potential collection biases, while also calling for focused research on environmental drivers of facultative cave occupation in Neotropical systems. These records highlight the need for further exploration and documentation of Colombia's cave-dwelling fauna, emphasizing the importance of caves as reservoirs of biodiversity, urging future studies to expand taxonomic surveys across cave microhabitats, and assess the conservation value of these ecosystems through species-specific dependency assessments.

Unlike other Amblypygi species, those of the genus *Charinus* tend to have more restricted distributions and smaller sizes, which contrasts with the broader distributions commonly seen in other larger Amblypygi, even though troglobitic species are typically larger when compared to other representatives of their respective taxonomic groups with epigean populations. These smaller species may be more adapted to confined cave environments and could be more diverse in Colombia than currently known. Members of Phrynidae are often classified as troglophile or trogloxene species (e.g. Armas 2015), without apparent morphological adaptations to the hypogean environment. Records of these species in caves are limited, with most known from single localities or individual caves, except perhaps for *H. cervinus*, which is known from at least two well-separated caves, without intermediate localities.

Most Amblypigi cave records are from the Eastern and Central Cordillera and the Caribbean Coast, regions with karstic or calcareous origins, as well as from the Serranía La Macarena/La Lindosa, where cave formations have a non-calcareous origin. This may reflect the limited exploration of karst regions in other parts of the country that have shown high karst potential, which may be due to the Racovitzan impediment (Ficetola et al. 2019), where knowledge gaps persist due to insufficient exploration of biodiversity in difficult-to-access systems and regions such as tropical caves.

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